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Systematics of the *Gomphales*: the genus *Gomphus* sensu stricto

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Abstract — *Gomphus* sensu lato (*Gomphales*) was described to include species of cantharelloid-gomphoid fungi that had 'merulioid' (wrinkled) hymenia and verrucose spores. *Gomphus* sensu stricto is currently characterized by unipileate to merismatoid (composed of several pilei) basidiomata, depressed funnel- to fan-shaped pilei, presence of clamp connections, and verrucose spores; it has three described species: *G. brunneus*, *G. clavatus*, and *G. crassipes*. Basidiomata and spore features are reliable identifiers of *Gomphus* sensu stricto that distinguishes the species from other genera in the *Gomphales*.

Key words — *Gloeocantharellus, Phaeoclavulina, Turbinellus*

Introduction

The genus *Gomphus* was originally proposed as a segregate from the genera *Clavaria*, *Geoglossum*, *Mitrula*, and *Spathularia* and described as "thickened, truncate, smooth, laterally plicate-venose, the pileus weakly developed" (Persoon 1797). No species were assigned to the genus when described. The first citation of a species for *Gomphus* came only when Gray (1821) described *G. clavatus* based on *Merulius clavatus* Pers., a species known to have merismatoid (composed of several pilei) basidiomata, orangish brown to violet pilei, violet hymenia, and verrucose non-anastomosed ornamented spores.

From the earliest citations of Persoon (1797) to the latest descriptions of Petersen (1971), the systematics and nomenclature of *Gomphus* have had a checkered history. Before Giachini (2004) analyzed the molecular phylogeny of 320+ collections of *Gomphus* sensu lato and related genera in the *Gomphales* and reviewed the systematics and nomenclatural history for this group, species of *Gomphus* sensu stricto were assigned to three different genera: *Cantharellus*

(Fries 1821), *Craterellus* (Fries 1838), and *Neurophyllum* (Doassans & Patouillard 1886).

The reduced number of distinctive morphological features and (more importantly) the lack of molecular data to clarify the systematics of this group have contributed to its confused classification. Nevertheless, the significant contributions by many taxonomists have led to a better understanding of the overall placement of gomphoid fungi.

Recently Giachini & Castellano (2011) presented a new classification for *Gomphus* sensu lato. Giachini (2004) and Giachini & Castellano (2011) emphasized that *Gomphus* sensu stricto is the only genus in the *Gomphaceae* with strictly violet, lavender-brown, or milky-coffee colored hymenia, distinguishing it from other representatives of *Gomphus* sensu lato (*Gloeocantharellus*, *Phaeoclavulina, Turbinellus*) characterized by orange, brown or greenish olive hymenia. Furthermore, all *Gomphus* species produce clamp connections and verrucose spores. The unique combination of these morphological characteristics separates *Gomphus* from other genera within the *Gomphales*.

Below we review the important diagnostic characters of *Gomphus* sensu stricto and provide a dichotomous key and complete descriptions of the three currently accepted species: *G. brunneus*, *G. clavatus,* and *G. crassipes*. For discussion on the nomenclatural history of *Gomphus* sensu lato see Giachini (2004), Giachini et al. (2010), and Giachini & Castellano (2011).

Materials & methods

Collections examined

Collections of *Gomphus* were obtained from BR, DAOM, FH, K, MICH, NYS, OSC, S, SFSU, TENN, and WTU (http://www.nybg.org/bsci/ih/ih.html). Since Dufour (1889) did not assign a type for *G. crassipes* and the only known collections (two) deposited at the herbarium RAB were not granted for loan, its description and further notes were taken from the relevant literature.

In addition to dried herbarium material, we examined fresh specimens of *G. clavatus* from northern California, Oregon, and Washington. These were collected mostly in late September to mid-December, the usual fruiting season. Therefore, colors for *G. clavatus* are based on fresh and dried material while for *G. brunneus* are based on dried material only.

After selected collections were photographed and macroscopic features recorded, they were dried within 24 h of collection with a forced-air food dehydrator set at 38–40°C, and deposited at OSC.

Habitat and fruiting patterns are based on information from the original descriptions and/or field observations.

Macroscopic characterization

Macroscopic features are based on original descriptions and herbarium notes supplemented by our own data on fresh or dried specimens. Features of the pileus,

hymenium, stipe, flesh, odor and taste were recorded whenever possible. Size of basidiomata may vary depending on conditions of the fruiting season, so the ranges of minimum and maximum sizes are presented as the range for 5–10 collections. Several specimens were cut longitudinally through the vertical axis to examine the context structure of pileus and stipe. Application of chemicals often used and referred to in the literature (Corner 1966, Petersen 1971) in describing species of *Gomphus* sensu lato proved of little value and so are not reported here.

Microscopic characterization

Features observed with a compound microscope were described from free-hand sections mounted in Melzer's reagent, 5% KOH, cotton blue, or H_2O. Structures were measured with an optical micrometer at ×1000 magnification, mostly in mountants. Hyphal wall thicknesses are recorded as 'thin' ≤0.5 µm and 'thick' >0.5 µm. The pileipellis and stipitipellis were examined in surface view. When material was available, dimensions were recorded from at least 3 specimens from each of at least 5 collections. Both mature and immature specimens were examined for developmental changes. Maturity was judged by the relative abundance of fully ornamented spores.

Spore shape was determined by the length-width ratio of 20–30 randomly selected spores (Kirk et al. 2008). Dimensions are given as: minlength–maxlength × minwidth–maxwidth, excluding ornamentation and apiculus. Immature or oversized spores were not included in the measurements, though variation was noted.

Taxonomy

Species are presented in alphabetical order. Descriptions include citation of all examined material and the herbarium where the type and other collections are deposited. Descriptions are based on notes available with collections, the observations made in this study, and literature reports.

Gomphus Pers., Tent. Disp. Meth. Fung.: 74 (1797) [non *Gomphus* (Fr.) Weinm.1826].

(For synonymy, see Giachini & Castellano 2011:186.)

Type species: *Gomphus clavatus* (Pers.) Gray 1821.

Basidiomata ≤18 cm tall, erect, unipileate to merismatoid, when merismatoid with two to several pilei arising from a single stipe. Pileus 4–18 cm wide, plane to depressed, fan- to funnel-shaped, flexuous, fleshy, dry, glabrous (*G. brunneus*) to subpruinose, covered with brown hyphae that form minute separate and distinct patches toward the margin but merge into a continuous felty tomentum over the disc (*G. clavatus*), rosaceous, sordid yellow to orange-brown, creamy violet, violet, brown; margin lacerate to crenate. Hymenium decurrent, wrinkled, generally longitudinally oriented, dichotomous, often to rarely anastomosing, reticulate to almost poroid (*G. brunneus*), especially near the stipe apex, more lamellate toward the margin of the pileus, violet, vinaceous brown to milky-coffee colored. Stipe ≤80 mm long, solid, cylindrical to tapering downward, generally dilating into the pileus, pale violet to brown, nearly black in *G. crassipes*, often pale red-brown where handled. Context

firm, pliable, often with anastomosing cavities, especially in *G. clavatus*, white, off-white, violet, pale rose, brownish pink on exposure. Odor faint to sweet. Taste mild to bitter. Spore print brown for *G. brunneus* and *G. clavatus*, not recorded for *G. crassipes*.

Pileipellis of scattered to fasciculate, simple or branched, rarely slightly inflated hyphae, in *G. clavatus* with pileocystidia; clamp connections present. Stipitipellis of parallel hyphae at surface, interwoven beneath, hyaline, ≤2 µm wide; clamp connections present. Pileus and stipe context of interwoven, hyaline hyphae 2.5–6 µm wide, generally uninflated except adjacent to the clamp connections. Hymenial trama of thin- to thick-walled hyphae; clamp connections present. Subhymenial trama of interwoven, hyaline hyphae ≤8 µm wide; clamp connections present. Basidia ≤100 µm long, 12 µm wide, clavate, in general with (2–)4 slightly divergent, slightly incurved sterigmata; clamp connections present. Hymenial cystidia absent. Basidiospores 7.5–17 × 3.5–7.5 µm, orange, yellow-brown to dark olive in mass, ellipsoid to obovoid; ornamentation verrucose, cyanophilic; apiculus eccentric (not recorded for *G. crassipes*).

Ecology & distribution: epigeous, solitary to gregarious or caespitose, in leaf litter or terrestrial. When gregarious, basidiomata are often separated by a few centimeters. Encountered in Africa, Asia, Europe, and North America.

Remarks: Defining boundaries for species within *Gomphus* sensu lato has been a constant challenge because of the lack of consistent morphological features. Only recently have morphology and molecular techniques combined to provide a natural classification for the *Gomphaceae*. Giachini et al. (2010) and Giachini & Castellano (2011) verified by molecular and morphological data that species of *Gomphus* sensu stricto (*G. brunneus, G. clavatus,* and *G. crassipes*) are in a lineage separate from all other species of *Gomphus* sensu lato. Accordingly, *Gomphus* sensu stricto is reduced to three species vs. the 35 formerly assigned to *Gomphus* sensu lato. Main features diagnosing *Gomphus* are the smooth to subpruinose pileus, wrinkled or poroid-like hymenium, and clamp connections. Species of *Gomphus* sensu stricto occur across the northern hemisphere and as far south in Africa as the Democratic Republic of the Congo.

Gomphus brunneus (Heinem.) Corner, Ann. Bot. Mem. 2: 116. 1966. Fig. 1

(For synonymy, see Giachini & Castellano 2011:186.)

Type: DEMOCRATIC REPUBLIC OF CONGO. Equateur, Binga, April 1928, *M. Goosens-Fontana 683* (BR A253).

Basidiomata ≤9 × 4 cm, unipileate, erect, clavate, truncate at apex. Pileus ≤4 cm wide, depressed to funnel-shaped, thick in the center, thin toward the ascending and somewhat lacerate margin, brown or occasionally more or less rosaceous, with paler tones in the center. Hymenium wrinkled, reticulate

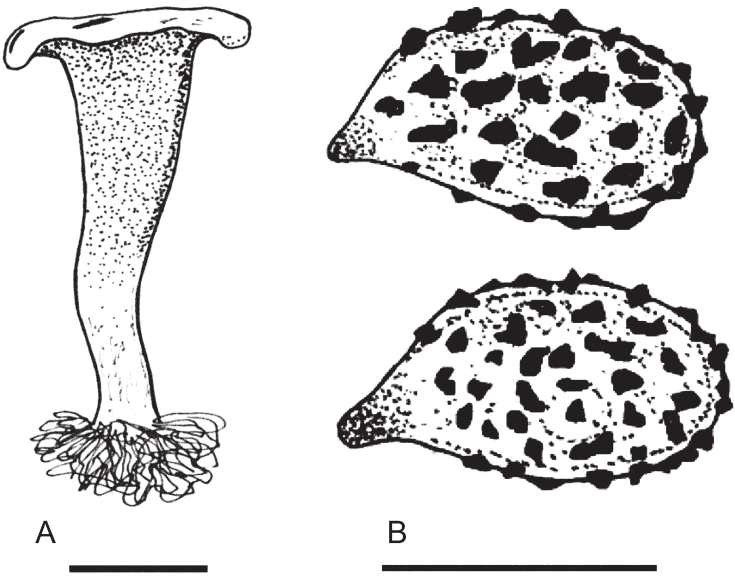

Fig. 1. *Gomphus brunneus*. A. Basidioma (bar = 2 cm). B. Basidiospores (bar = 5 µm).

to almost poroid, pale violet to milky-coffee colored. Stipe ≤80 mm long, tapered downward, dilating obconically into the pileus, brown, the base white tomentose. Context pliable, white, then brownish pink on exposure. Odor not recorded. Taste bitter. Spore print brown.

Pileipellis of scattered to fasciculate, simple hyphae; clamp connections present. Stipitipellis of hyaline hyphae ≤2 µm wide; clamp connections present. Pileus and stipe context of interwoven, hyaline hyphae 2.5–6 µm wide; clamp connections present. Hymenial trama of thin-walled hyphae; clamp connections present. Subhymenial trama of slightly thickened, hyaline hyphae 3–7 µm wide, with refractive walls; clamp connections present. Basidia 50 × 8 µm, with 2–4 sterigmata. Hymenial cystidia absent. Basidiospores 7.5–10 × 3.5–5 µm, yellow-brown in mass, ellipsoid to obovoid; ornamentation of cyanophilic warts arranged more or less in longitudinal rows; apiculus rounded, eccentric.

Ecology & distribution terrestrial, in leaf litter, on floor of dry forests of Cameroon (Roberts 1999), the Democratic Republic of Congo, and Uganda (Corner 1966, Roberts 1999).

Additional specimens examined: **UGANDA**: Gunda Forest, May 1918, *T.D. Maitland 275* (as *Gomphus clavatus* var. *parvisporus*; K 57307).

Remarks: *Gomphus brunneus* is distinguished by its simple basidiomata with smooth pilei, weakly wrinkled hymenia, clamped hyphae, and comparatively small basidiospores. Its morphology, distribution, and molecular profile make it unique (Giachini 2004, Giachini et al. 2010, Giachini & Castellano 2011).

Only two *G. brunneus* herbarium collections were available for examination. After studying the type, Roberts (1999) considered *G. clavatus* var. *parvisporus* from Uganda (described by Corner 1966 and said to occur in Europe and the western USA) a synonym of *G. brunneus*. Both species are macroscopically similar with unusually small verrucose spores and are known only from equatorial Africa. Heinemann (1958, 1959) reported two collections from forests of the Democratic Republic of Congo, Africa. Corner (1966) reported one collection (as *Gomphus clavatus* var. *parvisporus*) from Cameroon, while Roberts (1999) cited two collections from Cameroon obtained in 1996 and reported abundant basidiomata from the same location on the following year. Otherwise, the species appears to be restricted to the Democratic Republic of Congo and Uganda.

For several decades *Cantharellus pseudoclavatus* A.H. Sm. (Smith & Morse 1947) was classified under *Gomphus* sensu lato (Corner 1966). After analyzing the type collection (MICH 6916), however, Giachini (2004) concluded that it better fit *Cantharellus*. The main morphological character justifying its removal from *Gomphus* sensu lato was the presence of 8-spored basidia, a feature not found elsewhere in *Gomphus* but present in *Cantharellus*. Petersen (1971) had previously transferred the species to *Pseudocraterellus*, a genus which also lacks 8-spored sterigmata. Although Corner (1966) suggested *Gomphus clavatus* var. *parvisporus* occurs in Europe and is common in western USA, he mentioned only specimens obtained in Africa in his original description of that variety. *Cantharellus pseudoclavatus* is rare under conifers of the western USA and is definitely distinct from *G. brunneus*.

Gomphus clavatus (Pers.) Gray, Nat. Arr. Brit. Pl. 1: 638. 1821. Fig. 2

(For synonymy, see Giachini & Castellano 2011:187.)

Basidiomata ≤17 cm tall, unipileate at first and then merismatoid with ≤15 subpilei. Pileus ≤15 cm wide, the surface flat, subundulate, fan-shaped, glabrous to covered with brown hyphae that form minute separate and distinct patches toward the margin but merge into a continuous felty tomentum over the disc, orangish brown to overall creamy violet to dark violet; margin crenate. Hymenium surface wrinkled, generally longitudinally oriented, with or without discrete folds or pits, bright violet at the margin and junction with stipe and overall when immature, at maturity covered with spores and then paler (vinaceous brown). Stipe tomentose to hispid toward the base, glabrous above and there blending to pale violet, white at the base and where covered

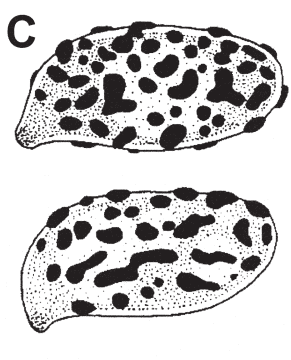

Fig. 2. *Gomphus clavatus*. A–B. Basidiomata. C. Spores (bar = 10 µm).

(soil, debris), often pale red-brown where handled. Context often with anastomosing cavities, violet around those, off-white to pale rose elsewhere. Odor faint or none. Taste mild. Spore print brown.

Pileipellis often crowded, thin-walled, scattered to fasciculate, with simple or branched hyphae, usually incrusted apically, with pileocystidia 3–4.5 µm wide, rarely slightly inflated, ≤5.5 µm, protruding 50–120 µm from the surface; clamp connections present. Hyphae and bases of pileocystidia often with brown amorphous deposits. Stipitipellis of periclinal and parallel, hyaline hyphae 1.5–2 µm wide at the surface, becoming interwoven beneath, with few projecting hyphae where stipe is glabrous, or fascicles of crowded hyphae where stipe is hispid; clamp connections present. Pileus and stipe context of thin- to slightly thick-walled, generally oriented on the long axis of the basidioma but profusely interwoven, hyaline hyphae 2.5–6 µm wide, generally uninflated except adjacent to the clamp connections, where it is slightly thick-walled (≤1 µm thick) and ≤12 µm wide. Hymenial trama hyphae more loosely interwoven than the rest of the context, undifferentiated from the subhymenial trama. Basidia 60–95 × 8.5–12 µm, clavate, collapsing after spore discharge, hyaline, with (2–)4 slightly divergent, slightly incurved sterigmata ≤10 µm long; clamp connections present at base. Hymenial cystidia not observed. Basidiospores (9–)10–15(–17) × 4–7.5 µm, orange in Melzer's reagent, dark olive in mass (KOH), ellipsoid to obovoid, contents weakly cyanophilic; ornamentation of cyanophilic warts, usually in discrete, raised patches that give an undulate appearance to the spore surface; apiculus prominent, eccentric.

Ecology & distribution: solitary, gregarious to caespitose, when gregarious often separated by a few centimeters, terrestrial. Generally in conifer forests and suggested to form mycorrhizae with species of *Abies* (Pantidou 1980) and *Picea* (Agerer et al. 1998). Known from Austria (Petersen 1971), Canada (East and West, Petersen 1971), China (Corner 1966), Czech Republic (Kluzák 1994), France (Doassans & Patouillard 1886), Greece (Petersen 1971), Italy (Petersen 1971), Japan (Corner 1966), Lithuania (Urbonas et al. 1990), Mexico (Petersen 1971), Pakistan (Corner 1966), Poland (Adamczyk 1996), Russia (Bulakh 1978, Bulakh & Govorova 2000), Spain (Fernando Sanchez, pers. comm., 10 Oct. 1999), Sweden, Switzerland (Petersen 1971), Turkey (Sesli 1997), and the USA (especially northwestern/northeastern and into the Appalachian Mountains). Loans were requested from herbaria located in most of these countries but several did not respond, so our examination of specimens is restricted to those listed under collections examined.

Additional specimens examined: **CANADA. British Columbia,** Vancouver Island, 15 October 1962, *M. Pantidou* (DAOM 91369). Quebec, Duchesnay, 26 Aug. 1938, *H.S. Jackson* (DAOM 8624). **SWEDEN**: Uppsala, Södermanland, Handen, 4 Sep. 1998, *L. Kerwién* (S); Fiby Urskog, 20 Sep. 1998, *A. Taylor* (S). **UNITED STATES. California,** Del Norte Co., Del Norte Coast Redwoods State Park, 9 Dec. 1999, *M.A.*

Castellano (OSC 97685); Jedediah Smith Redwoods State Park, 17 Nov. 1961, *D. Isely 1479* (WTU), and 12 Nov. 1966, *H.D. Thiers* (SFSU 17740); Siskiyou Nat. Forest, Smith River, 30 Nov. 1937, *A.H. Smith 9243* (MICH); El Dorado Co., Pleasant Valley, 22 October 1967, *D.E. Stuntz 14410* (WTU); Mendocino Co., 5 Nov. 1961, *D. Largent 71* (SFSU); Aleuria Glenn, 14 Nov. 1967, *R.H. Petersen* (TENN 33256); Aleuria Glenn, along Rd. 404, 25 October 1986, *M. Seidl 2120* (WTU); Jackson State Forest, 5 Nov. 1967, *R.H. Petersen and H.D. Thiers* (TENN 33174), and 8 Dec. 1999, *A.J. Giachini, M.A. Castellano and E. Nouhra* (OSC 97679, 97680, 97681, 97682, 97683, 97684). **Idaho,** Bonner Co., Priest River, Binarch Creek, 9 Sep. 1966, *R.H. Petersen* (TENN 32166); Priest River Experimental Forest, Canyon Creek Road, 11 Nov. 1939, *A.H. Slipp 621* (MICH). **Massachusetts,** Essex Co., Gloucester, Aug. 1877, *unnamed collector* (FH). **New York**, Saratoga Co., Ballston Lake, Branch, 1879, *C.H. Peck* (holotype of *Cantharellus brevipes*; NYS). **Oregon,** Benton Co., Siuslaw Nat. Forest, Mary's River, 24 October 1999, *S. Ashkannejhad* (OSC 97622); Clackamas Co., Wemme, 23 Sep. 1946, *A.H. Smith 23644* (MICH); Coos Co., South Slough, 23 Sep. 1985, *C. Ardrey 800* (WTU), and 3 Sep. 1992, *C. Ardrey 1806* (WTU); Lane Co., Cougar Reservoir, Road 19, 27 Nov. 1999, *A.J. Giachini* (OSC 97671, 97672, 97673, 97674, 97675, 97676, 97677); Eugene, 30 October 1999, *unnamed collector* (OSC 97646); H. J. Andrews Experimental Forest, Lookout Mt., Rd. 1506, 23 October 1999, *A.J. Giachini* (OSC 97616, 97620, 97669, 97670, 97678); H. J. Andrews Experimental Forest, 23 October 1999, *A.J. Giachini* (OSC 97617), 5 Nov. 1999, *A.J. Giachini* (OSC 97656), and 7 Nov. 2000, *Y. Yano* (OSC 97694); Oakridge, Road 1934, 15 Nov. 1999, *A.J. Giachini* (OSC 97668); Willamette Nat. Forest, 25 October 1999, *C. Lefevre* (OSC 97623); Linn Co., Sweet Home, 4 Nov. 2000, *A.J. Giachini* (OSC 97696, 97698); Willamette Nat. Forest, Pamela Lake Trail head, 2 Nov. 1999, *A.J. Giachini* (OSC 97624); Marion Co., Detroit Lake, Road 46, 15 Nov. 1999, *A.J. Giachini* (OSC 97667). **Washington**, Chelan Co., Lake Wenatchee, 7 Nov. 1980, *D.E. Stuntz 21131* (WTU); Clallam Co., Morse Creek camp, 17 October 1942, *D.E. Stuntz 1245* (WTU); Olympic Mountains, 30 October 1931, *H.S. Hotson* (WTU); Kings Co., Snoqualmie Nat. Forest, Asahel Curtis Nature Trail, 4 Aug. 1992, *G.R. Walker 10600* (WTU); Lewis Co., Mt. Rainier Nat. Park, Bumping Lake, October 1937, *D.E. Stuntz 759* (WTU); Pierce Co., Mt. Rainier Nat. Park, Lower Tahoma Lake, 23 Sep. 1948, *D.E. Stuntz 4732* (WTU); Old Tahoma campground, 23 Sep. 1960, *D.E. Stuntz 12000* (WTU); Mt. Rainier National Park, Tahoma Creek, 18 Aug. 1948, *D.E. Stuntz and A.H. Smith 4003* (WTU); Mt. Rainier Nat. Park, Tahoma Creek, 23 Sep. 1960, *D. Isely 1257* (WTU).

Remarks: *Gomphus clavatus* has traditionally been placed in a monotypic subgenus (*Gomphus* subg. *Gomphus*) based on morphological features (Corner 1966). However, molecular studies by Giachini (2004) and Giachini et al. (2010) support its placement together with *G. brunneus* and *G. crassipes* in *Gomphus* sensu stricto and suggest it to be phylogenetically closely related to species of *Gloeocantharellus*. Petersen (1971) noted that these two genera share several morphological similarities, the most striking of which is that both exhibit the same reaction to 10% KOH applied to the basidioma pileus. In reference to *G. clavatus* Petersen (1971) stated, "the normal color immediately becomes a most unique salmon-yellow, almost precisely the normal color of the pileus and stipe of *Gloeocantharellus purpurascens* (Hesler) Singer." The pileus surface tomentum of *G. clavatus* is composed of pileocystidia, just as in *G. purpurascens*,

and, even though the pileocystidia of the two species differ in shape and orientation, they have a similar brown agglutinating substance. Despite these similarities, the molecular evidence shows *Gomphus* and *Gloeocantharellus* to be in distinctly different, but related lineages (Giachini et al. 2010).

Other taxa in the *Gomphaceae* share the merismatoid habit of *G. clavatus,* notably *Phaeoclavulina grandis* (Corner) Giachini, *P. guadelupensis* (Pat.) Giachini, *P. subclaviformis* (Berk.) Giachini, and *P. viridis* (Pat.) Giachini and *Gloeocantharellus dingleyae* (Segedin) Giachini, *G. novae-zelandiae* (Segedin) Giachini, and *G. pallidus* (Yasuda) Giachini.

Gomphus crassipes (L.M. Dufour) Maire, in Maire & Werner, Mém. Soc. Sci. Nat. Maroc 45: 81 (1937). FIG. 3

(For synonymy, see Giachini & Castellano 2011:187.)

Lectotype designated here, Pl. 13, in L.M. Dufour, Rev. Gen. Bot. 1: 357–358. 1889.

BASIDIOMATA ≤18 cm tall, unipileate or occasionally merismatoid. PILEUS 4–18 cm wide, plane to slightly depressed in the center, funnel-shaped to fan-shaped, non hygrophanous, sordid yellow to orangish brown; margin subundulate. HYMENIUM decurrent, wrinkled, occasionally anastomosing, dichotomous, violet. STIPE 40–70 × 25–45 mm, cylindrical to slightly tapering downward, almost entirely underground, central or lateral, nearly black. CONTEXT firm, pale violet, marbled in the stipe with violet tones. ODOR sweet. TASTE not recorded. SPORE PRINT color not recorded.

All HYPHAE 5–8 µm wide; clamp connections present. BASIDIA 70–100 × 8–10(–12) µm, clavate, with (2–)4 straight sterigmata. HYMENIAL CYSTIDIA absent. BASIDIOSPORES (11–)13–15(–17) × 5.5–6(–7) µm, pale orange in mass, ellipsoid to obovoid; ornamentation of cyanophilic, fine warts; data on apiculus not recorded (Dufour 1889, Maire 1914).

ECOLOGY & DISTRIBUTION: on the ground, generally grouped, in conifer forests in Algeria (Dufour 1889, Maire 1914, Maire & Werner 1937), Morocco (Malençon 1958), and Spain (Miguel À. Pérez-De-Gregorio i Capella, pers. comm., 5 Jan 2004).

REMARKS: As the only known collections are at herbarium RAB in Morocco, and our loan request was denied due to the material's fragile condition, our description is based on Dufour (1889), Maire (1914), and Maire & Werner (1937). Dufour (1889), who did not cite any collection or herbarium for the type species, stated that "cette espèce est assez voisine du *Cantharellus brevipes* Peck." As *C. brevipes* is a synonym of *G. clavatus*, in effect Dufour related *G. crassipes* to *G. clavatus*, with similar macro- and microscopic characteristics, differing only by the violet to marbled violet color of the context, which is violet, off-white to pale rose in *G. clavatus.* However, its overall spore size and

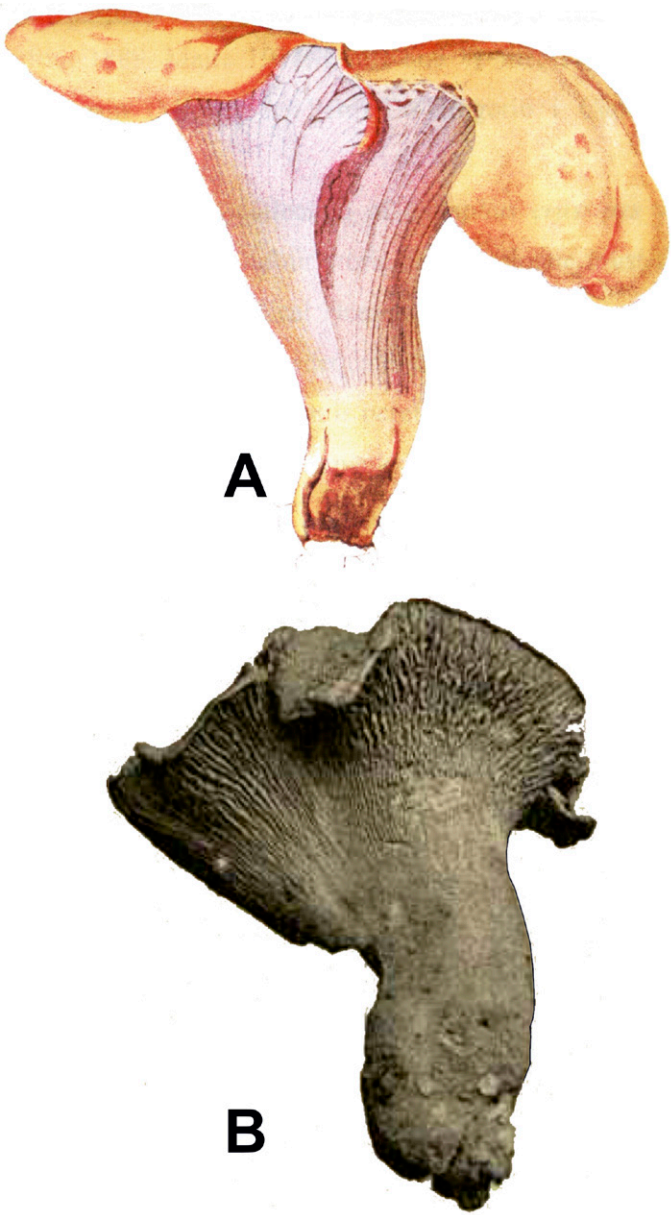

Fig. 3. *Gomphus crassipes*.
A. Basidiomata [from Maire (1914: Pl. VII.2)].
B. Dried basidiomata [modified from Dufour (1889; Pl. 13), with permission].

geographic distribution suggest that *G. crassipes* is distinct from *G. clavatus* (Giachini et al. 2010).

Only a few other references to *G. crassipes* are observed in the literature. Maire (1914), who transferred Dufour's *C. crassipes* to *Neurophyllum*, provided a detailed description and excellent drawing of its basidiomata and spores (Maire 1914) and subsequently (Maire & Werner 1937) transferred the species to *Gomphus*. Later Malençon (1958) called attention to the putative relationship of *G. crassipes* to the coral fungi, especially to *Ramaria,* but observed that Maire's drawings were not good representations of what Dufour (1889) had described as *C. crassipes* and that in particular the were not those suggested by Dufour. This species "pulls too much into the yellows and reds" according to Malençon (1958), who described *G. crassipes* as having a pale ocher to rose pileus surface. However, as seen for other species of *Gomphus* sensu lato, (e.g., *G. clavatus*) the color of both pileus and hymenium surface can vary considerably. For *G. clavatus*, for example, the pileus surface can be orangish brown to overall creamy violet to dark violet. It is possible that Maire (Maire & Werner 1937) observed a color variant of *G. crassipes*.

Because the designated lectotype does not adequately characterize the species, an epitype is desirable. However, we refrain from designating an epitype since no herbarium specimen is available and Malençon (1937) challenged the Maire's (1914) excellent illustration. A fresh collection (preferably from Morocco) that can provide DNA sequences would be an ideal candidate for epitypification.

Key to species

1a. Basidiomata initially unipileate, then becoming merismatoid with ≤15 subpilei; pileus fan-shaped, orangish brown, creamy violet to dark violet; hymenium wrinkled, violet, vinaceous brown, lavender-brown;
Asia, Europe, North America ..... *G. clavatus*

1b. Basidiomata unipileate to merismatoid; pileus depressed, funnel-shaped, occasionally fan-shaped, brown to rosaceous, sordid yellow to orangish brown; hymenium wrinkled, reticulate to almost poroid, violet to milky-coffee colored;
Africa, Spain 2

2a. Spores 7.5–10 × 3.5–5 µm, verrucose; basidiomata unipileate; pileus brown or occasionally rosaceous; hymenium slightly wrinkled, reticulate to almost poroid, pale violet to milky-coffee colored;
Cameroon, Democratic Republic of Congo, Uganda ..... *G. brunneus*

2b. Spores (11–)13–15(–17) × 5.5–6(–7) µm, finely verrucose; basidiomata occasionally merismatoid; pileus sordid yellow to orangish brown; hymenium wrinkled, violet;
Algeria, Morocco, and Spain ..... *G. crassipes*

Discussion

Gomphus was originally described to include cantharelloid-gomphoid species that produced basidiomata resembling those of *Cantharellus*. The recent molecular analyses of Giachini et al. (2010), which sharpened generic and species concepts within the *Gomphaceae* and revealed *Gomphus* sensu lato as non-monophyletic, support redistribution of those into *Gomphus* sensu stricto, *Gloeocantharellus, Phaeoclavulina,* and *Turbinellus*. Only three original species are retained within *Gomphus* sensu stricto — *G. brunneus* characterized by somewhat funnel-shaped pilei and *G. clavatus* and *G. crassipes*, characterized by fan- to funnel-shaped pilei.

Gomphus clavatus, widely distributed in the northern hemisphere, is believed to form ectomycorrhizae with species of *Abies* (Pantidou 1980) and *Picea* (Agerer et al. 1998). It is the most easily identified of the three species, due primarily to the size and color of its basidiomata. Since the development and implementation of the Northwest Forest Plan in the United States (USDA/USDI 1994a,b, 2000, 2001), *G. clavatus* has been considered rare and potentially restricted to old-growth forests of the Pacific Northwest (PNW), requiring all federal and state land to be surveyed for the species before any management activity could be approved.

Both *G. brunneus* and *G. crassipes* are known only from a few collections from Africa and Spain, as noted above.

Morphologically *Gomphus* sensu stricto is readily separated from the other gomphalean genera based on the violet, violet-brown to orangish brown colors and fan- to somewhat funnel-shaped basidiomata pilei.

Species of *Gomphus* sensu stricto most resemble those of the resurrected genus *Phaeoclavulina* (Giachini & Castellano 2011), which share fan- to funnel shaped pilei and clamp connections. However, they differ based on spore ornamentation, with most *Phaeoclavulina* species diagnosed by echinulate, subreticulate, or reticulate spores in contrast to the strictly verrucose spores of *Gomphus*.

Even though all *Turbinellus* species were assigned to *Gomphus* until recently, they share only few morphological characters, most notably spore ornamentation. They differ in basidiomata shape, color, and presence of clamp connections (absent in *Turbinellus*).

Gomphus and *Gloeocantharellus* occupy an important position in the evolution of the fungi in the *Gomphales*. Molecular analyses (Giachini et al. 2001, Giachini et al. 2010, Humpert et al. 2001), indicate *Gloeocantharellus* and *Gomphus* as ancestral to all other genera within the *Gomphales*. The two genera share spore shape and ornamentation and (for some *Gloeocantharellus* species) clamp connections.

Unavailability of samples restricted more in-depth evolutionary inferences of *Gomphus* to other genera in the *Gomphales*. Additional sampling, especially

for *G. crassipes*, is necessary to determine whether subgeneric arrangements exist within *Gomphus* sensu stricto and to infer higher-level relationships to other members of the *Gomphales*. A complete discussion on the evolutionary relationships and implications of this taxonomic classification in relation to other members of the *Gomphales* can be found in Giachini (2004), Hosaka et al. (2006), and Giachini et al. (2010).

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